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Role of Visual Cues in Host Searching Behaviour of *Exorista sorbillans* Widemann, a Parasitoid of Muga Silk Worm, *Antheraea assama* Westwood

Dipsikha Bora · Bhabesh Deka

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Abstract Visual cues are known to be used by numerous animal taxa to gather information on quality and location of resources. The present work was carried out to understand if visual cues are involved in host localization by E. sorbillans and if so, does an associative learning influence host localization behaviour. The Uzi fly, Exorista sorbillans Widemann is an endoparasitoid of the silkworm, Antheraea assama Westwood and a serious threat to the silk production industry in general. Associative learning in the fly was studied by using green and orange coloured paper disk in presence or absence of a reward, sugar or silk worm larvae. Training for the rewards in the learning experiment was given for 2 days for 30 min at regular intervals. Flies positively associated colored paper disks with the presence of hosts which indicated that they might employ visual learning of microhabitats associated with host habitats, or the hosts themselves. Our results showed that in context of host foraging, training with colours as host associated cues was more reliable than training with colours in the absence of hosts. Thus associative learning may be considered to be an essential component for survival of Exorista sorbillans.

Keywords *Antheraea assama* · *Exorista sorbillans* · associative learning

Introduction

In the life of many organisms, the act of finding a potential host in a complex natural environment plays a key role in their survival. Phytophagous insects use cues associated with their host plants while parasitoids take help of a variety of host or habitat derived cues to identify appropriate search arenas (Prokopy et al. 1973; Vinson 1984; Owens and Prokopy 1986; Godfray 1994; Bleeker et al. 2009). Once landed on the host arena, the parasitoids effectively use their senses to assess more specific cues to determine the host species suitable for oviposition or feeding (Beehler et al. 1993; Yamawaki and Kainoh 2005). Insect parasitoids are reported to use a variety of olfactory, visual and auditory cues to locate their hosts (Cade 1975; Walker 1993; Feener et al. 1996; Feener and Brown

D. Bora (✉) · B. Deka
Department of Life Sciences, Dibrugarh University, Dibrugarh, Assam, India
e-mail: dipsikhabora03@yahoo.com

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1997; Morehead and Feener 2000; Alvarado et al. 2009). Many insect parasitoids may also discriminate between the parasitized and nonparasitized host, an important behaviour for solitary parasitoids that do not prefer to lay eggs in host already parasitized by other females (van Lenteren 1981). Shape, size, colour and movement of the host are usually reported to be used as visual cues by the insect parasitoids. In several instances host movement exhibit overriding effect on host recognition by the dipterans (Fukushi 1989; Aluja and Prokopy 1993; Morehead and Feener 2000 and Stireman 2002b) although the mechanism of filtering the movement based non-host stimuli is not clear.

Learning in animal causes change in behaviour that occurs as a result of experience. Learning may be used primarily in development of host searching behaviour, provided the relevant informations received contribute to its fitness (Singer and Thomas 1996; Parmesan et al. 1995; Papaj and Prokopy 1989; Dukas 1998). Associative learning is the process in which learning occurs through association of stimuli with reward. A parasitoid that can learn cues associated with their host microenvironment might have an increased chance of future host location and thereby increase its reproductive success (Oliai and King 2000). Probably such insects come under strong selection pressure to be able to decide on the best environments for development of their progeny. Learning by the parasitic wasp *Microplitis croceipes* Cresson (Hymenoptera: Braconidae) occurs with stimuli other than odor, such as pattern, shape and color (Wackers and Lewis 1999). Associative learning with odour has been reported in certain dipterans (McCall and Eaton 2001; Tomberlin et al. 2006). Apple maggot fly (*Rhagoletis pomonella*) (Aluja and Prokopy 1993) and blow flies, *Lucilia cuprina*(Fukushi 1985, 1989) are reported to use visual cues in host location and oviposition. A few studies have been done to understand mechanism of host location in certain tachinid parasitoids which indicate their learning ability (Monteith 1956; Roth et al. 1978, 1982; Stireman 2002b). Several of the works done are related to their ability to act as biological control agent (Nakamura 1997). Morehead and Feener (2000) reported on detection of motion by the dipteran parasitoid, phorid flies while Stireman (2002a) reported on learning of visual cues and use of both visual and olfactory cues by *Exorista mella.* The Uzi fly (*Exorista sorbillans*) is a generalist parasitoid. Its adults feed on nectar, honey etc. In the present study, attempt was made to determine the role of visual cues and associative learning used in short-range host location and acceptance by this dipteran parasitoid, *Exorista sorbillans* using *Antheraea assama,* the producer of golden yellow muga silk as its host. It lays eggs on the body of the silk worm larva. The maggots hatching out of the eggs spend their lives within the body of the silk worm larva and when mature emerge out of silk cocoon by piercing to undergo pupation on loose soil. It would be interesting to understand how this notorious parasitoid learns to locate the silk worms.

Materials and Methods

Experimental Animal

Uzi fly maggots were collected from silkworm culture maintained in Govt. sericulture farms of Assam, India and were cultured in laboratory condition of 22–30 °C temperature and 12:12(±1) night/day cycle. The newly emerged adult Uzi flies were kept in wooden boxes covered with net (32×41×26 cm). Each terrarium was provided with separate petri

dishes containing water, sugar cubes sprinkled with yeast-bacto powder. Second day old male and female adults were kept together in a common chamber to ensure mating. As pre oviposition period in the species is 2–3 days all females used in the training experiments were 4 to 7 days old to ensure that they had the opportunity to mate and develop fertile eggs. Prior to use in experiments, care was taken not to expose the females to either honey or larval hosts to prevent the flies from having any learning experience.

Experiment 1: Innate Colour Preference (from Choice Test)

This experiment was done to determine whether females have an innate preference for green or orange colour. Prior to testing females were not exposed to any of the colours. In a common chamber both the colours were placed and each fly was allowed to choose either of the two colours, green or orange without giving a reward. When the fly entered the chamber time recording was started using stopwatch till 10 min. As soon as the fly touched any one of the petri dishes the test was terminated and if a fly did not touch the petri dish within 10 min, the latency period (time to contact the petri dish) was recorded as 10 min (or 600 s.). Time spent in each coloured disk was recorded. A total of 20 mated females were tested. Comparison of preference for the green or orange colour was done by chi-square test.

Experiment 2: Coloured Paper Disk with Larva

To test the learning ability of *Exorista sorbillans* for association of visual cues with hosts, mated female flies were subjected to training sessions with *Antheraea assama* caterpillars associated with green and orange paper disks. The colours green and orange were chosen because they are considerably separated in wavelength along the visible spectrum and the green colour was reported to be preferred by other species of the genus *Exorista* (Ichiki et al. 2011). Training of flies were conducted by placing flies in clear plastic hexagonal chambers (20×36×11 cm). Petri dish (8.7 cm diameter) containing either a green paper disk or orange paper disk was placed in each training chamber. A fifth instar silk worm larva was placed over the coloured paper disk as reward. 30 females were selected for training for each colour and placed in the chambers individually. A female fly was released into the chamber from the top in each training session. To prevent learning of a location of petri dishes, the position of the dishes in each chamber was changed after each oviposition exercise. Each fly was allowed to oviposit on a caterpillar and just after oviposition the caterpillar was removed from the container and a fresh caterpillar was placed on the same coloured disk. In case the caterpillar left the petri dishes, they were immediately placed back to the original location. Each fly was trained for a period of minimum 30 min to 1 h or until they parasitized three caterpillars. The training session was continued for two consecutive days with 24 h gap period in between. After second training session the flies were allowed to take rest for half an hour and just after half an hour the behaviour of each fly was examined in a choice and no-choice test. The test was conducted for 10 min in the same type of chamber as used in the training sessions.

NO-Choice Test During the tests each fly was presented with an empty petri dish containing randomly chosen coloured disk and subsequently with an alternate colour disk. Using a stopwatch the time was recorded for a maximum of 10 min. As soon as the fly entered the

chamber the time was recorded till it touched the petri dish and once it touched the petri dish, the test was terminated. If a fly did not touch the petri dish within 10 min the latency period (time to contact the petri dish) was recorded as 10 min (or 600 s). To test the differences in response between the trained and the untrained colour, the non-parametric test, Mann–Whitney ANOVA was used.

Choice Test In a common chamber, both the colours were placed and each fly trained for a particular colour (orange or green) was allowed to choose any of the colours for landing. When the fly entered the chamber, the time was recorded up to 10 min. As soon as the fly touched any one of the petri dishes, the test was terminated and if a fly did not touch the petri dish within 10 min the latency period (time to contact the petri dish) was recorded as 10 min (or 600 s.) Twenty mated trained females were tested. Comparison of preference between the trained versus untrained colour was done by a non-parametric Mann–Whitney ANOVA test.

Experiment3: Coloured Paper Disk with Honey

To test the learning ability of *Exorista sorbillans* for association of visual cues with honey (food) as reward, mated female flies were subjected to training sessions for honey associated with green and orange paper disks. Training of flies was conducted similarly as in experiment 1. But on each disk, in place of the host larva was placed a cotton ball soaked with honey. Thirty females were selected for training and placed in the chambers individually. Each fly was trained for a period of minimum 30 min to 1 h or until they landed on honey ball for three times. This training session was continued for two consecutive days with 24 h gap period in between. After second training session each trained fly was allowed to take rest for half an hour and immediately after, the behaviour of each fly was examined in a choice and no-choice test. Each test was conducted for 10 min in the same type of chamber used during the training sessions.

Choice and no-choice test was carried out by following the same methods as experiment 1.

Analyses

Data were analyzed using software package SPSS 13. Due to the repeated use of same individuals in the above mentioned experiments of choice and no- choice, all analysis was conducted in a paired fashion. Non-parametric Mann–Whitney ANOVA and chi-square test were used in all experiments to analyze the significance of the responses. All statistical analysis used for the above experiments were judged with p value (0.05) at 95 % significant level.

Analysis for Preference for Host Larva Versus Honey

This analysis was aimed to determine which was the more preferable reward for associative learning—larval host or honey? The analysis was based on the raw scores of the results of experiment 1 and 2. Chi-square test was performed for determining the strength of preference (Tables 1 and 2).

Table 1 First colour chosen by *E. sorbillans* females when trained with larval host as reward (statistics: Mann–Whitney ANOVA)

Trained colour	First colour chosen	Latency to contact the disk (seconds)	F	P
Green	Green	50±0.012		
	Orange	213±0.106	5.821	0.030
Orange	Green	295±0.089		
	Orange	56±0.022	8.27	0.021

Results

Experiment 1: Innate Colour Preference (from Choice Test)

The mated female flies did not show an innate colour preference for green over orange colour ($p>0.05$). The first colour chosen by the females was considered as an indication of the colour on which they would spend maximum of time. But the latency period and the time spent by the mated flies on the first colour green versus orange was almost equal (Fig. 1a and b).

Experiment 2: Response of Flies to Coloured Paper Disk with Larva

No Choice Test In test with coloured disks, the latency period i.e. the time taken till first contact with the green coloured disk in which it was trained was 50 s and in case of the alternate colour (orange) the latency period was 213 s (Fig. 2a).

In the other experiment in which flies were trained with orange coloured disk, the latency period for the trained colour was 56 s and the latency period for the flies in case of alternate colour (green) was 295 s (Fig. 2b).

The difference in response to the trained and the untrained colour was significant for both green trained ($P=0.03$) and orange trained flies ($P=0.021$) (Table 1).

Choice Test

In case of choice test when the flies were trained with green colour all the flies preferred green coloured disk and the average latency period was 155 s. None of the flies opted for orange coloured disk (Fig. 3a and b).

When the flies were trained with orange colour, 80 % of the flies preferred trained coloured disk and the average latency period was 162 s. 20 % of the flies did not show any response (Fig. 3a and b).

Table 2 First colour chosen by *E. sorbillans* females when trained with honey as reward (statistics: Mann–Whitney ANOVA)

Trained colour	First colour chosen	Latency to contact the disk (seconds)	F	P
Green	Green	262±0.0418	8.37	0.014
	Orange	545±0.233		
Orange	Green	316±0.234	6.89	0.023
	Orange	169±0.031		

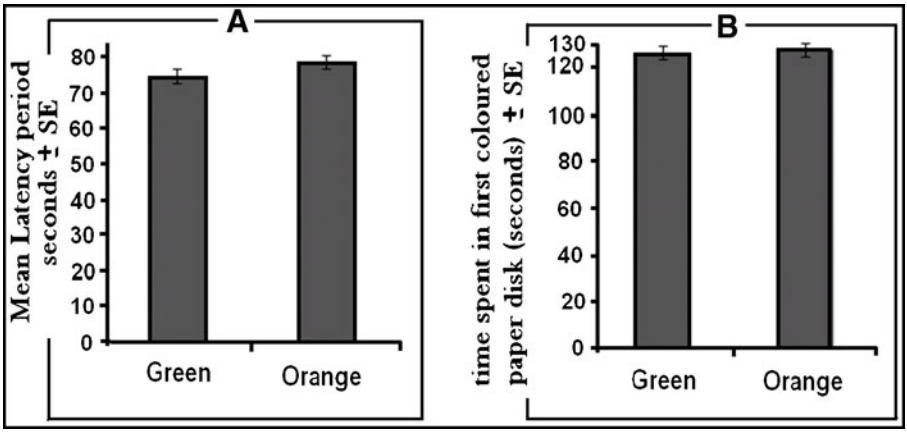

Fig. 1 **a** Comparison of the mean (±SE) time to contact the trained paper disks by female *E. sorbillans* (p>0.05 Chi-square test). **b** Comparison of time spent by female *E. sorbillans* on the green versus orange coloured disk (both trained colour) (p>0.05 Chi-square test)

The total number of flies that made contact with the coloured disk on which they were trained within the test duration was significantly higher than the number that made contact with the alternative coloured disk (Mann–Whitney ANOVA for latency U=42.0 and for colour preferred U=12.0, P=0.002).

Experiment 3: Response of Flies to Coloured Paper Disk with Honey

No Choice Test

In test with coloured disks with honey, the latency period i.e. the time taken till first contact with the green coloured disk in which it was trained was 262 s and in case of the alternate colour (orange) the latency period was 545 s (Fig. 4a).

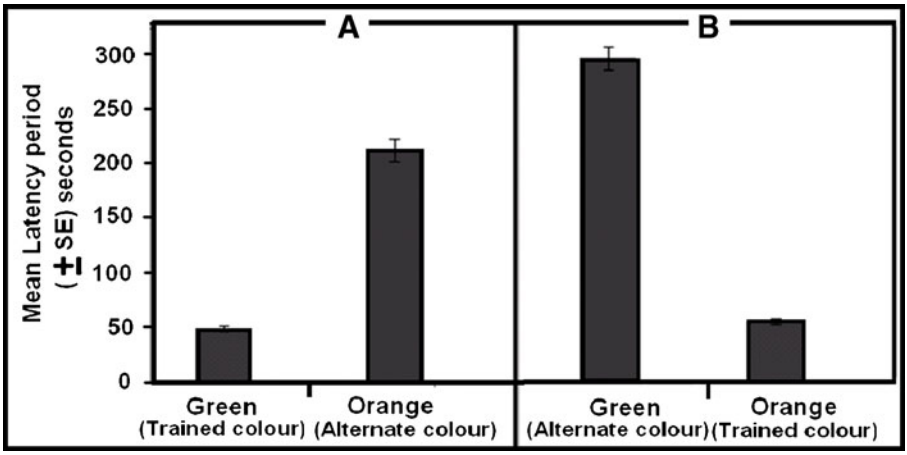

Fig. 2 The mean (±SE) time to contact the paper disk in no-choice test (**a**: trained in green and **b**: trained in orange) by female *E. sorbillans* (N=20) when trained with larvae (as reward)

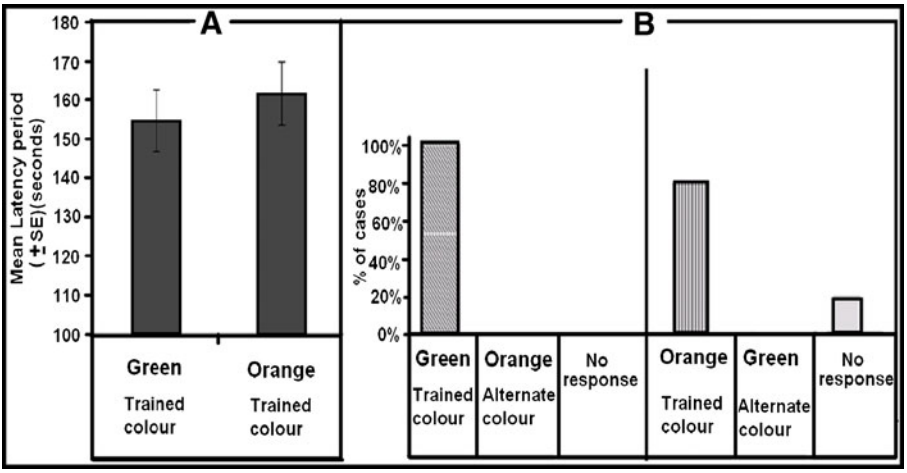

Fig 3 **a**: The mean (±SE) time to contact the trained paper disks by female *E. sorbillans* (*N*=20 for each colour) when trained with larvae (as reward) in choice test. **b**: % of trained female *E. sorbillans* which touch the trained colour, alternate colour as well as no response during choice test when trained with larvae (as reward)

In the other experiment in which flies were trained with orange coloured disk, the latency period for the trained colour was 169 s and the latency period for the flies in case of alternate colour (green) was 316 s (Fig. 4b).

The difference in response to the trained and the untrained colour was significant for both green trained flies (*P*=0.014) and orange trained flies (*P*=0.023) (Table 2).

Choice Test

In case of choice test when the flies were trained with green colour 80 % of the flies preferred trained coloured disk and the average latency period was 159 s. 20 % of the flies did not show any response.

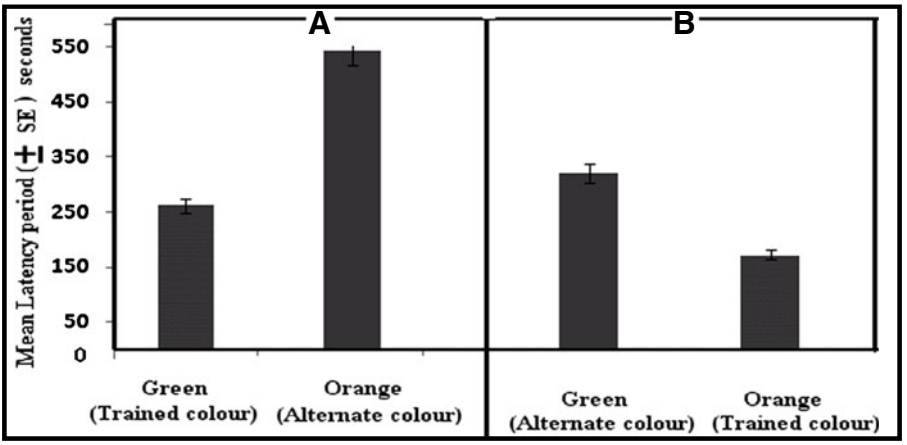

Fig. 4 The mean (±SE) time to contact the paper disk (**a**: trained in green and **b**: trained in orange) by female *E. sorbillans* (*N*=20) when trained with honey (as reward)

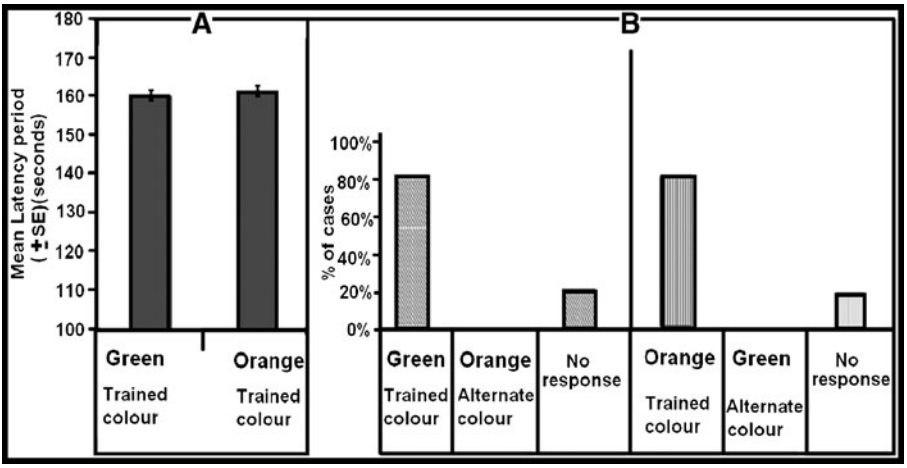

Fig. 5 **a**: The mean (±SE) time to contact the trained paper disks by female *E. sorbillans* (*N*=20 for each colour) when trained with honey (as reward) during choice test. **b**: % of trained female *E. sorbillans* which touch the trained colour, alternate colour as well as % of no response during choice test when trained with honey (as reward)

When the flies were trained with orange colour, 80 % of the flies preferred trained coloured disk and the average latency period was 160 s. 20 % of the flies did not show any response.

The total number of flies that made contact with the coloured disk on which they were trained within the test duration was significantly higher than the number that made contact with the alternative coloured disk (Fig. 5a and b). (Mann–Whitney ANOVA for latency U=48.0 and for colour preferred U=14.0, P=0.004).

Preference for Host Larva Versus Honey

When analysis was done to evaluate the preference for larva versus honey as reward, the females took 56±0.186 s to touch the trained coloured disk when the reward was larval host for oviposition (p<0.05) while they took 295±0.151 s when the reward was honey. Thus the flies were quicker in touching the trained coloured disk when the reward was larval host for oviposition in comparison to condition when the reward was honey (Fig. 6).

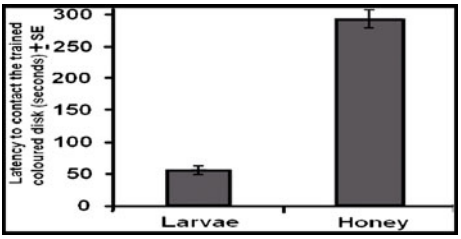

Fig. 6 The mean (±SE) time to contact the trained coloured paper disk by female *E. sorbillans* (*N*=20 for each reward) when the reward was both larvae and honey. Chi-square value: 12.389; df: 2 (*P*=0.002)

Discussion

Results obtained from the experiment showed that, the total number of flies that made contact with the coloured disk on which they were trained, either with larval host or with honey as reward was significantly higher than the number that made contact with the alternative coloured disk. Based on this finding, the parasitoid, *E. sorbillans* may be considered to have preferred the trained colour in their host or food finding exercise. Thus, they exhibited discrimination learning and associative learning for visual cues. However, what characteristics of the coloured disk were used for discrimination could not be ascertained from this experiment. Some related taxa eg. *Lucilia* was reported to be able to learn the wavelength irrespective of brightness (Fukushi 1989). Spectral sensitivity is known to play important role in colour recognition in Hymenopterans also (Wardle 1990; Shafir 1996).

For studying associative learning using the principles of Pavlovian conditioning the organism should not have innate preference for the conditioned stimulus used. Innate colour preferences have been reported in honey bees (Giurfa et al. 1995), blow flies (Fukushi 1989) and certain butterflies (Weiss 1997). Tephritid dipterans were earlier reported to be attracted to green, orange and yellow colours than other colours (Lopez-Guillen et al. 2009). In contrast, in the present study, the female *E. sorbillans* showed no innate preference for green and orange colour. Similarly the parasitic wasp *Nasonia vitripennis* was also reported to show no innate preference to yellow and blue colour (Oliai and King 2000).

The larger proportion of green trained flies (69.23 versus 54.54) that responded to test treatments may indicate that this colour is more easily associated with the hosts. But among the flies which responded to test treatments given by using the two different colours, no significant difference was observed in their ability to learn to associate either of the colour with the hosts [i.e., no effect of colour (P=0.088) or colour x treatment (P=0.226)]. Earlier *Exorista japonica* was shown to prefer green colour with the host plant odour (Ichiki et al. 2011). A preference for common foliage colour such as green and yellow has been reported in many herbivorous insects (Prokopy and Owens 1983) and in certain Hymenopteran and Dipteran parasitoids as well (Goff and Nault 1984; Romeis et al. 1998; Jonsson et al. 2005; Ma et al. 1992).

As discussed above, *E. sorbillans* females learned to associate colour with hosts and/or honey. Besides honey bees, some other hymenopterans have also been shown to associate colour with their hosts or food. The parasitoid wasps for example, *Itoplectis conquisitor* and *Exeristes roborator* (Hymenoptera: Ichneumonidae) also learned to associate colour with hosts (Arthur 1966; Wardle 1990). Additionally *Polybia occidentalis* (Hymenoptera: Vespidae) was reported to learn to associate colour with sugar (Shafir 1996). Besides, learning for colour using food as reward has also been reported in some other dipterans, lepidopterans, and orthopterans (Wardle 1990; Weiss 1997). In this present study , based on latency period observed in experiment 2, the females may be said to have preferred the trained coloured disk more when the reward was larval host for oviposition (p<0.05) as against the condition when the reward was only honey. In *N. vitripennis,* hosts elicited a stronger preference than honey and the reason was considered to be due to the fact that the females could both feed and oviposit on the same. In order to avoid the question of internal motivation for the choices food or oviposition, necessary care was taken in setting up the experiment. In the experiment, the flies used were not only mated and in a ready state for

oviposition, but were also deprived of food for 12 h. Thus they were kept hungry for both oviposition and food prior to the experiment. But if ovipositional need is a stronger motivation force than hunger then the question needs to be further addressed. The results presented in Figs. 2 and 3 reveal that the latency period in the no choice test was less when the reward was larva. The reason might be due to skipping of important steps used in host finding when only a single choice was available for oviposition (Van Driesche and Murray 2004). In nature the adults get exposed to different carbohydrate sources and when they were subjected to single choice test for honey the latency period was longer (Figs. 4 and 5). This might be due to the rare situation of single choice they were subjected to for decision making. In general the flies have greater relative frequency of encountering carbohydrate versus larva. Insect's choice for oviposition or food is also known to be governed by chemical perception. In Tinbergen's experiment, odour of the flower was realized to be the attracting force (Tinbergen 1984). Although host associated cues have strong impact on the mated fly's visual system comprising of large eyes characteristic of dipterans and other animals in general are known to use complex signals in location of their hosts for oviposition, food and enemies (Rowe 1999; Candolin 2003). While pollinators use multi-component floral signals including both colour and scent in foraging (McNeely and Singer 2001; Kulahci et al. 2008), the parasitoids for the purpose of oviposition use cues emanated from multitrophic levels like herbivore induced host plant volatiles, volatiles from host insects and their frass (Dicke and van Loon 2000; Nufio and Papaj 2001). As explained by Leonard and his co-workers (Leonard et al. 2011), complex floral display provides pollinators with multiple independent samples of information about a signal associated with a reward. When an animal takes a decision through learning, both learning and the subsequent decision depends on the informations obtained which are relevant to the animal's fitness (Parmesan et al. 1995; Mcneely and Singer 2001). Consequently learning also reduced the time taken in finding nectar in Mcneely and Singer' experiments. According to the 'redundant signals' hypothesis of Hebets and Papaj (Hebets and Papaj 2005), sampling both visual and olfactory stimuli allows insects to be more certain about the identity of a rewarding. In the present investigation, apart from visual information when honey was assessed by the parasitoid probably the chemical information content offered was only a single signal while during the assessment of larva as reward multiple chemical signals were received as live hosts release blends of different volatile chemicals. The multiple chemical signals might have offered stronger identifying cues than the single chemical signal. Presumably, in nature the relative frequency of encountering hosts is less in comparison to carbohydrate. This may also explain the stronger influence of host in associative learning. Learning of visual cues by Tachinid was reported earlier also. According to Tanaka et al. (1999), the female *Exorista japonica* recognizes the host for oviposition through tarsal examination for obtaining information on texture of the ovipositing surface and curvatures of host model. Parasitic hymenopterans like Ichneumonid wasp, *Campoletis sonorensis* were reported to recognize host texture or shape with antennal receptor (Vinson 1985). *Apanteles melanoscelus,* a parasitoid of gypsy moth used hairs on host surface in their recognition process (Weseloh 1974). In the present study since the texture of host larval skin and the cotton ball soaked with honey was different the physical factor may also play role in enhanced preference for the larval host. Stireman (2002a) demonstrated learning of host associated visual and chemical cues in *Exorista mella* which is a generalist parasitoid. As reported by Steidle and Van loon (2003), both generalists and specialists may exhibit innate preference to

infochemicals irrespective of dietary specialization. Besides, host pursuit in parasitoid *Exorista* spp. is also reported to be controlled by host movement (Yamawaki et al. 2002) and visual detection of motion was explained to be a close range indicator for presence of a suitable host in case of *E. mella* (Stireman 2002b). Taking all facts together, associative learning may be considered to be an essential component for survival of *Exorista sorbillans.* This generalist parasitoid uses different physical and chemical characters associated with the host larva in its host location and assessment process for oviposition. The fly is a serious parasitoid of the silkworm and is reported from all the silk producing areas of Asia including India, Southern China, Bangladesh, Japan, South Korea, Thailand and Vietnam (Ghosh 1949). Although in case of domesticated silkworms, the infestation by the parasitoids can be controlled to a certain extent by using physical barrier, in case of semi domesticated silkworms like *A. assama* and wild Tasar silk worms in which case larvae are maintained outside in the field, control of infestation by *E. sorbillans* is difficult. Determination of the cues used by the parasitoid in host finding might open the avenue for trapping the flies leading to its successful management in an environment friendly way.

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